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Females and males maintain similar-sized, stable territories between breeding and nonbreeding seasons in a tropical oriole (*Icterus icterus*)

Karan J. Odom,[1,2]* Evangeline M. Rose,[1] Michael T. Hallworth,[3,4] Oscar A. Díaz-Marrero,[5,6] and Kevin E. Omland[1]

ABSTRACT—Territories provide important breeding and nonbreeding resources for many bird species. Most songbird territory research has been conducted in temperate regions during the breeding season, a situation in which primarily males appear to defend territories and for only a few months. In the tropics, however, both females and males of many species may defend territories year-round and for multiple years, yet few studies have verified this with marked or radio-tagged birds. To assess territory stability in both sexes between seasons and years, we examined similarity in territory size, location, and overlap with neighbors between the breeding and nonbreeding seasons and 2 subsequent breeding seasons in a tropical resident songbird, the Troupial (*Icterus icterus*). Mated females and males maintained similar-sized, tightly overlapping territories that had considerably less overlap with neighbors than each other. Both sexes maintained similar-sized territories in the breeding and nonbreeding seasons and between years. The location of territory centers and extent of overlap with neighbors was also similar between seasons and years. Divorce and/or territory switching appeared to be uncommon, but upon disappearance of a mate, both sexes often replaced the mate to maintain the territory. Our work quantitatively verifies for both sexes the year-round territorial behavior expected for this and many tropical species. Such territory similarity and stability likely plays a role in song, plumage, and sex role similarities also seen in female and male Troupials. *Received 13 August 2018. Accepted 28 January 2019.*

Key words: female territoriality, *Icterus icterus*, nonbreeding season, tropical songbird, year-round territoriality

Hembras y machos mantienen territorios estables de tamaños similares en las temporadas reproductiva y no-reproductiva en el turpial tropical *Icterus icterus*

RESUMEN (Spanish)—Los territorios proveen recursos reproductivos y no-reproductivos para muchas especies. La mayoría de la investigación sobre el territorio de las aves canoras se ha llevado a cabo en regiones templadas durante la temporada reproductiva, situación en la que los machos parecen defender territorios solo por algunos meses. En los trópicos, sin embargo, machos y hembras de muchas especies pueden defender territorios durante todo el año por múltiples años, si bien son pocos los estudios que han verificado este hecho por medio de aves marcadas o con radiotransmisores. Para determinar la estabilidad de territorios en ambos sexos entre estaciones y años en un ave tropical residente, el turpial *Icterus icterus*, examinamos la similitud en tamaño del territorio, localidad y traslape con aquél de sus vecinos entre las temporadas reproductiva y no-reproductiva en dos estaciones reproductivas subsecuentes. Parejas de hembra y macho mantuvieron territorios de tamaño similar que se traslapan entre sí de manera estrecha y que mantienen un traslape considerablemente menor con el de sus vecinos. Ambos sexos mantienen territorios de tamaños similares en las temporadas reproductiva y no-reproductiva, así como entre años. Asimismo, la localización del centro de los territorios y la extensión del traslape con sus vecinos también fue similar entre temporadas y años. El divorcio y/o el intercambio de territorios parecen ser poco comunes, aunque con la desaparición de su pareja, ambos sexos frecuentemente encontraron un reemplazo para mantener el territorio. Nuestro trabajo verifica, de forma cuantitativa, y para ambos sexos, el comportamiento territorial durante todo el año que es esperado para ésta y muchas especies tropicales. Dicha similitud y estabilidad de territorios juega un papel en las similitudes en el canto, plumaje y papel de los sexos que pueden observarse en turpiales hembras y machos.

Palabras clave: aves canoras tropicales, temporada no-reproductiva, territorialidad de hembras, territorialidad todo el año

Most studies on territorial behavior of songbirds have been conducted at temperate latitudes. At those latitudes, males generally defend breeding territories that exist only a few months of the year to attract females and rear offspring (Nice 1941, Catchpole and Slater 2008). In the tropics, however, paired male and female songbirds of many species appear to defend multi-purpose territories year-round and often for multiple years (Greenberg and Gradwohl 1986, Stutchbury and Morton 2001). Researchers have argued that these kinds of tropical behaviors should be considered the norm rather than the exception (Morton 1996, Stutchbury and Morton 2001). Recent years have seen an increase in studies on male and female wintering, nonbreeding territoriality in Neotropical migrants (e.g., Morton et al. 1987, Parrish and

[1] Department of Biological Sciences, University of Maryland, Baltimore County, Baltimore, MD, USA
[2] Cornell Laboratory of Ornithology, Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, USA
[3] Department of Geography and Environmental Systems, University of Maryland, Baltimore County, Baltimore, MD, USA
[4] Smithsonian Conservation Biology Institute – Migratory Bird Center, Washington, DC, USA
[5] Cabo Rojo and Laguna Cartagena National Wildlife Refuges, U.S. Fish and Wildlife Service, Boqueron, Puerto Rico
[6] Current address: Luquillo, Puerto Rico
* Corresponding author: kjo43@cornell.edu

Sherry 1994, Brown and Sherry 2008, Hallworth et al. 2011). Yet few studies have verified territory stability between the breeding and nonbreeding season in tropical, year-round residents (exceptions include Greenberg and Gradwohl 1986, 1997; Morton et al. 2000, Fedy and Stutchbury 2004, Gill and Stutchbury 2006). No studies that we are aware of on tropical, monogamous songbirds have radio-tracked males and females to determine breeding and nonbreeding season territoriality over multiple years.

Year-round territoriality is likely an important factor in the evolution of elaborate female and male traits and improved knowledge of tropical bird biology, in general, is necessary for resolving broad questions about avian life histories (Slater and Mann 2004, Macedo et al. 2008; Tobias et al. 2011, 2016). Shared territory and resource defense appears to have led to similarly elaborate plumage, song, and combined duets in both sexes in tropical regions (Lebas 2006, Tobias et al. 2012). Specifically, the evolution of duets appears to be tied to year-round territoriality (Tobias et al. 2016). Thus, female and male trait elaboration may be directly shaped by year-round resource defense (Tobias et al. 2012). Yet, the tropics encompass a wide variety of habitat types, which can be seasonally variable (Stutchbury and Morton 2001, Macedo et al. 2008). Therefore, formally documenting tropical bird biology, including the dynamics and extent of year-round territoriality in both sexes, is an important contribution to elaborate trait evolution and many other aspects of avian biology (Macedo et al. 2008, Tobias et al. 2012).

Empirical evidence of territory stability and male and female territoriality exist, but studies specifically documenting similarity of female and male territory size or stability in year-round tropical residents are confined to a small number of species and localities (Greenberg and Gradwohl 1997, Morton et al. 2000, Fedy and Stutchbury 2004, Gill and Stutchbury 2006, Stouffer 2007, Osmun and Mennill 2011). Studies on territory stability in tropical species demonstrate that year-round territoriality is typical, but reveal variation in the duration and conditions dictating territory tenure (Morton et al. 2000, Fedy and Stutchbury 2004, Gorrell et al. 2005, Gill and Stutchbury 2006, Stouffer 2007). Several studies have shown that both males and females participate in territory defense, but do not document territory sizes or tenure (e.g., Levin 1996a, 1996b; Hall and Magrath 2000, Logue and Gammon 2004, Mennill 2006, Templeton et al. 2011, Dahlin and Wright 2012, Dowling and Webster 2015, Odom and Omland 2018). A single study, on Rufous-and-white Wrens (*Thryophilus rufalbus*), shows that male and female territory sizes are similar and mates' territories overlap considerably (Osmun and Mennill 2011). Most research on tropical territoriality, however, has focused on dispersal, territory acquisition, and territory switching (e.g., Morton et al. 2000, Fedy and Stutchbury 2004, Gill and Stutchbury 2006, Carro et al. 2016). Throughout the tropics, there are a wide range of territory types and behaviors that vary with diet and across taxa (Stutchbury and Morton 2001). Therefore, documenting species- and sex-specific variation in territorial behavior using marked and radio-tracked populations is ultimately valuable for our understanding of sex role similarity and the evolution of male–female ornamentation.

To assess similarity of female and male territories and territory stability, we compared territory size, location, and neighbor overlap of male and female color-banded, radio-tagged Troupials (*Icterus icterus*). We also document and discuss instances of individual replacement and territory switching and/or divorce. Troupials are a tropical resident oriole in which both females and males sing, duet, and appear to actively defend territories (Odom et al. 2016, 2017). They are described as territorial year-round and are assumed to maintain territories over multiple years (Jaramillo and Burke 1999). However, fruit comprises a large part of their diet, so territories could shift seasonally or when resources are scarce, as in other frugivorous species (Stutchbury and Morton 2001).

Thus, our study tests 2 sets of alternative hypotheses. If Troupials are indeed territorial year-round, and use their territories for both breeding and nonbreeding activities, then we predict similar-sized territories in similar locations between the breeding and nonbreeding season. Similarly, if both males and females participate in defense of the same territory, we predict similarly sized territories with high overlap between mated males and females. Finally, if Troupials maintain territories over multiple years, we expected territory sizes and locations to be similar between years (subsequent breeding seasons).

Alternatively, if territories in Troupials mostly function during the breeding season, then we predict more overlap between neighbors in the nonbreeding season. In addition, we would expect less within-pair overlap in territory boundaries in the nonbreeding season. Finally, if territorial behavior and boundaries fluctuate between seasons, we predict territory locations and boundaries to shift between years.

Methods

Fieldwork was conducted in Cabo Rojo National Wildlife Refuge in southwestern Puerto Rico (17°590N, 67°100W). We collected territorial data over 3 field seasons: 22 April–29 June 2013, 3 April–1 July 2014, and 5 November–18 December 2014. These periods correspond to 2 breeding seasons and one nonbreeding season. Breeding by Troupials at our study site coincides with the wet season, which typically begins in late April or early May, followed by a short dry period and a second bout of breeding from July to September. The dry, nonbreeding season typically begins in October and lasts until April.

Data collection

All individuals included in the study were mated pairs of Troupials. To ensure sufficient data for estimates of territory size and center, we only included individuals or mates of individuals with more than 20 data points in at least one season. On average, birds included in the study had a total of 90 ± 7.9 SE data points and 46 ± 2.9 SE data points per season. This resulted in data for 20 males and 18 females across all 3 periods, which comprised 11 territories in summer 2013, 13 territories in summer 2014, and 12 territories in fall 2014. Most territories were observed all 3 field seasons. A table summarizing sample sizes for each individual per season is included as supplementary material. The full dataset is deposited at Movebank.org under study VenezuelanTroupial _Odom_PuertoRico. As described in Odom et al. (2016), all Troupials were banded with individual and sex-specific color bands. Sex was assigned in the field according to wing length and later confirmed by breeding behavior and molecular sexing (Griffiths et al. 1998). Troupials were also fitted with VHF radio transmitters to aid in locating and identifying individuals (Biotrack models Pip Ag386 and Ag393) during summer and fall of 2014. All GPS locations were taken as UTM with either a Garmin eTrex H or GPS Kit for iPhone. Users of both units waited for location accuracy to reach 5–10 m for each point before collecting GPS coordinates.

GPS points were primarily collected during 1 h observation sessions of Troupial vocal behavior, but were also gathered opportunistically when banded birds were resighted during observation sessions at other territories, while scouting for missing birds or unoccupied territories, or during routine nest checks. During 1 h observation sessions, the male and female of a pair were each followed separately by 2 independent observers. We collected GPS coordinates for every location where each focal bird perched. These observations were repeated throughout the season (5–8 sessions per season with 8–12 points typically collected per session) such that an equal number of observations were collected per pair. Observations were conducted sunrise to noon and balanced so that each pair was monitored an equal number of times throughout the morning (Odom et al. 2017). Opportunistic sightings occurred primarily in the last 3 h before sunset and were regularly alternated among the different territories. Autocorrelation can be a concern with territory data gathered continuously within a single period (Legendre 1993). However, we gathered data at different times and on multiple days. Also, Troupials often covered large distances per observation (multiple 100–200 m flights) to perch locations that were stereotyped and often repeated across visits. Therefore, we are confident we captured a biologically meaningful range of locations naturally frequented by the birds (Solla et al. 1999).

Spatial analyses

Spatial analyses were conducted in R (R Core Team 2015). We calculated 3 main variables: (1) territory size, (2) location, and (3) overlap with neighbors. These variables were compared between sexes, seasons (breeding 2014 and nonbreeding 2014), and years (breeding 2013 to breeding 2014). In addition, we assessed the amount of territory overlap of mates to determine similarity of male and female territories. We also

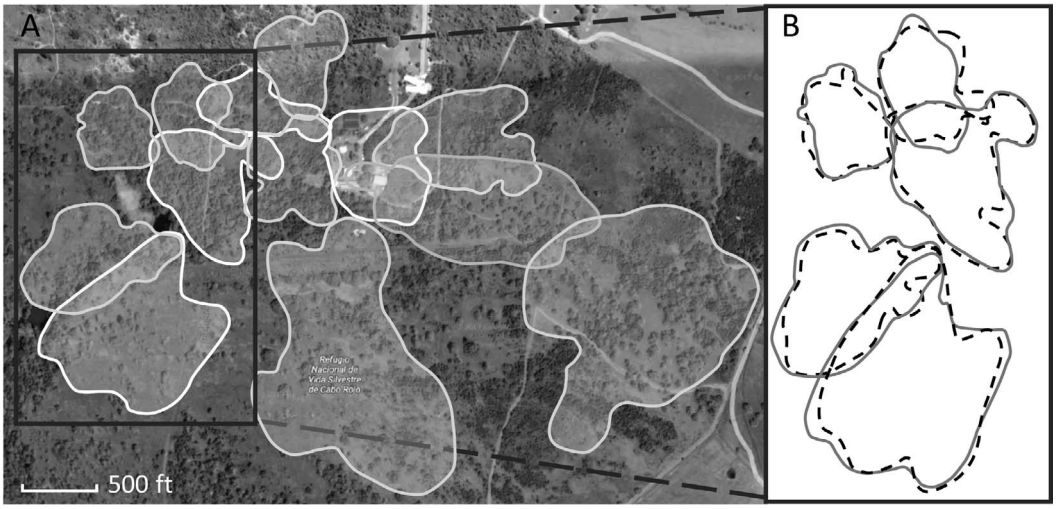

Figure 1. (A) Locations of 2014 breeding season Troupial territories on Cabo Rojo National Wildlife Refuge, Puerto Rico. Territory outlines (white) based on combined male and female 95% kernel density estimates. (B) Zoomed-in view of 5 Troupial territories showing overlap of male (solid gray) and female (dashed black) territories.

present raw values for instances of divorce and/or territory switching and replacement.

Territory sizes were determined using the 95% kernel density estimates (KDE) calculated from location data using least squares cross-validation to estimate bandwidth (Barg et al. 2005) in the ks package in program R (Duong 2007). We evaluated territory overlap between mates for males and females separately by calculating percent overlap of each male with his mate and each female with her mate. We also calculated the overlap between each bird and their nearest territory neighbor. We defined nearest neighbors as individuals with the shortest Euclidean distance between each other's territory centroids (based on this definition, the nearest neighbor for males vs. females was not always the same for mated pairs). To evaluate consistency of territory location, we examined the distance territory centers shifted between seasons and years, calculated as the distance between centroids of territory polygons. We defined the centroid of each territory as the geometric center of each polygon. We used this metric because it appeared to give the best estimate of center for Troupial 95% KDEs. To evaluate whether territory centers of individuals shifted a biologically meaningful distance, we compared individual shifts in territory centroids to the distance between each territory and the nearest neighbor's centroid.

Statistical analysis

Sex-specific analyses indicated that males and females did not differ significantly in territory size and neighbor overlap, so we included males and females together in subsequent analyses of season and year for these 2 variables. Therefore, we used 2-sample *t*-tests to compare territory size and overlap between sexes, seasons, and years using the t.test function in R (R Core Team 2015). For analyses comparing male and female centroid distance and for territory overlap compared to nearest neighbors, we conducted ANOVAs using the anova function in R (R Core Team 2015). We used a *P*-value threshold of $P < 0.05$ as statistical significance for all analyses. Values are provided as means ± SE.

Results

Territory size, location, and overlap

Males and females—Male and female Troupial territory sizes were similar (average territory size: male = 7.5 ± 1.3 ha, female = 6.8 ± 1.2; $t = 0.43$, df = 44.96, $P = 0.66$; Fig. 1, 2A). Territories of mated pairs also had very similar shapes and locations (Fig. 1). Mates overlapped most of each

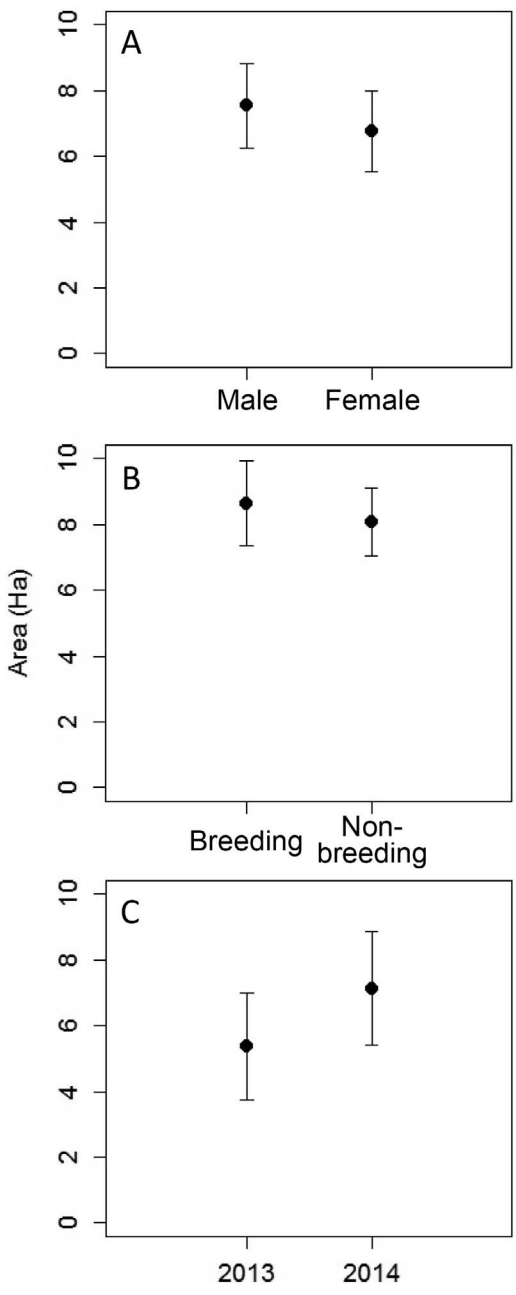

Figure 2. Troupial territory sizes were similar between (A) males and females, (B) the breeding and nonbreeding seasons, and (C) 2 consecutive years (breeding seasons).

other's territories (average overlap of mate's territory: male = 91.6%, female = 78.9%, sexes combined = 80.9%), which was significantly greater than the amount of overlap of either sex with territory neighbors ($f = 167.48$, df = 2, $P < 0.01$). Territory centers of mates were on average 26.4 m from one another, which was significantly closer than either was from nearest neighbor territory centers (201.2 m, $t = -13.10$, df = 89.36, $P < 0.01$). Both sexes also overlapped their neighbors' territories to similar extents (male = 0.18 ± 0.03 ha [18.1%], female = 0.16 ± 0.03 ha [15.9%]; Fig. 1, 3A). This overlap was significantly less than the size of an average territory ($f = 9.89$, df = 2, $P < 0.01$).

Between seasons and years—Troupials maintained similar-sized territories in both the breeding and nonbreeding seasons and between years (between seasons: $t = 0.35$, df = 46.25, $P = 0.73$; between years: $t = 0.73$, df = 25.91, $P = 0.47$; Fig. 2B, C). The amount of territory overlap between Troupials and their neighbors was also similar between seasons ($t = -1.08$, df = 36.76, $P = 0.29$; Fig. 3B) and years ($t = 0.91$, df = 32.60, $P = 0.37$; Fig. 3C). Territory locations were also highly stable (Fig. 4). Troupial territory centers moved very little between seasons and years, as shown by much shorter distances between individual territory centers in consecutive seasons or years than the average distance between neighboring territory centers (between seasons: $t = -6.35$, df = 41.71, $P < 0.01$; between years: $t = -3.15$, df = 17.22, $P < 0.01$; Fig. 4).

Divorce and territory turnover

Divorce and/or territory switching appeared to be low. We directly observed divorce and/or territory switching only once in 3 field seasons: a female left her mate and moved to an adjacent territory where she joined an existing male territory holder whose mate recently disappeared. In addition, we observed 6 other disappearances of individuals between seasons and years (4 males, 2 females). Two disappearances (one male, one female) were due to known death (remains found with radio transmitter). In all other disappearances, the missing bird was not seen subsequently in the study area. In 5 of 6 of these disappearances, the remaining territory owner maintained the territory and obtained a new mate. Only the mates of one missing female and the territory-switching female remained unmated and lost their territories. In 4 instances of mate replacement, new arrivals were known

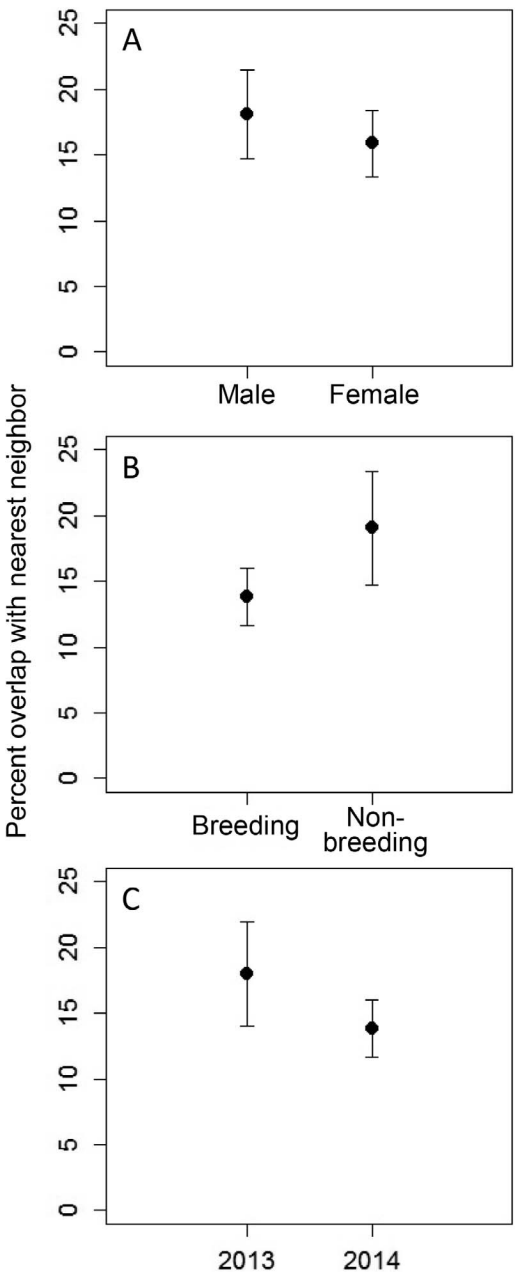

Figure 3. The percent overlap of Troupials with nearest territory neighbors was similar between (A) males and females, (B) the breeding and nonbreeding seasons, and (C) 2 consecutive years (breeding seasons).

floaters (banded individuals that appeared to be unmated—repeatedly seen in flocks or alone), previously sighted near or adjacent to the territory.

Discussion

Troupial territories were similar between sexes and were stable between seasons and across years. Mates shared very similar territory boundaries and stayed together defending the same territory in both the breeding and nonbreeding seasons and between years, matching our predictions for year-round territorial behavior. Thus, our findings fit better with the hypothesis that territories in Troupials function more for year-round resource acquisition rather than the alternative hypothesis that these territories mostly function during the breeding season. There was little turnover in mates or territories, and when this occurred it seemed to be related to loss of a mate rather than divorce. Both males and females remated after loss of a mate to maintain their same territory. Mate replacements were usually by nearby floater individuals, as seen in other year-round territorial species (Smith 1978).

Similarity of territory size and high territory overlap of mates is expected for tropical, socially monogamous species with similar sex roles, but may be particularly expected in duetting species, like the Troupial (Stutchbury and Morton 2001, Gill and Stutchbury 2006, Odom 2016). The Rufous-and-white Wren, also a tropical, monogamous, duetting species, showed similar patterns of territory size and overlap between mates (Mennill and Vehrencamp 2005, Osmun and Mennill 2011, Douglas et al. 2012). A major function of duets is territory defense, so tight territory overlap seems especially likely when mates jointly defend their territory (Hall 2004, Mennill and Vehrencamp 2008, Dahlin and Benedict 2014, Odom et al. 2017). Similarity of territory size or overlap between mates could therefore provide insight into the extent of joint territory defense, sex-role similarity, or pair cooperation. Comparing the similarity of territory size and overlap between mates for a variety of duetting species could reveal interesting trends pertaining to the extent of cooperation or coordination among mates. Interestingly, in Troupials, we also saw some overlap with territory neighbors (over 20% for some individuals some years). This may be because Troupials are frugivores and high densities of fruit at certain times and locations may lead to trespassing by or inability to fully exclude neighbors from nearby food resources. Our vocal

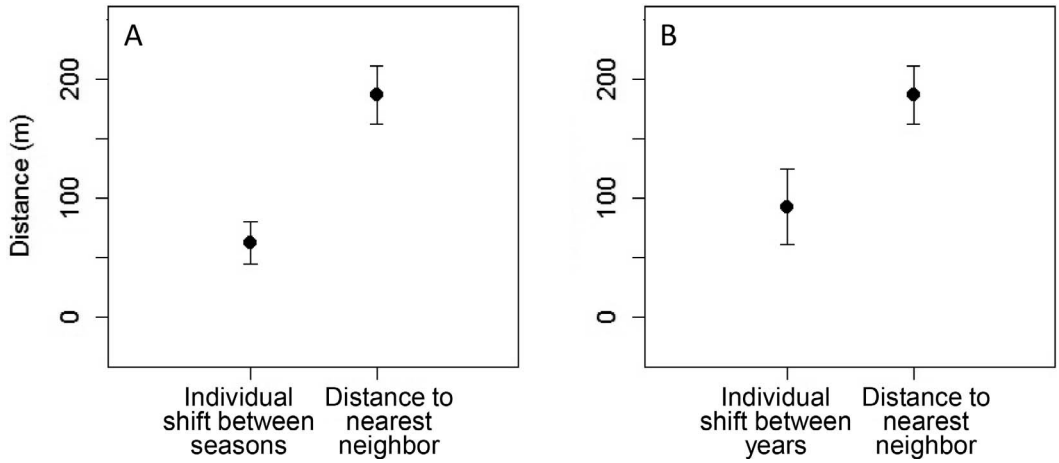

Figure 4. The distance individual Troupial territory centers shifted between (A) breeding and nonbreeding seasons and (B) consecutive years was small compared to the distance between nearest neighbor Troupial territories.

behavioral research indicates that Troupials defend their territories with duets (Odom and Omland 2018), which we regularly observed at territory boundaries. Our study with radio-tracked marked pairs provides strong quantitative data to add to our understanding of tropical monogamous territoriality.

The extent of year-round territoriality, specifically territory stability between breeding and nonbreeding seasons, is relevant to the evolution of elaborate female and male traits. In the tropics, food or breeding resources may be seasonally scarce, and maintaining a year-round territory may be important for survival as well as reproduction (Stutchbury and Morton 2001, Clutton-Brock 2009, Clutton-Brock and Huchard 2013). Defense of year-round resources may require participation by both sexes, selecting for elaborate traits in both sexes (Tobias et al. 2012). This may be especially true for Troupials, which depend on seasonally variable food resources (Jaramillo and Burke 1999). Female and male Troupials sing and duet in both the breeding and nonbreeding seasons and duet rates are higher in the nonbreeding season (Odom et al. 2016). Combined vocalizations, such as duets, are particularly common in year-round territorial species (Tobias et al. 2016). Therefore, competition for year-round resources may also specifically select for duets over solo vocalizations (Odom et al. 2015, Tobias et al. 2016). Quantifying the extent to which territories are stable year-round could be important to determine what drives the evolution of elaborate traits, especially elaborate female and collective behaviors (Rosvall 2011; Tobias et al. 2012, 2016).

Troupials exhibited the stable territorial behavior expected for a tropical, year-round territorial species (Stutchbury and Morton 2001). However, territory studies following marked tropical residents between seasons and years are rare and have revealed deviations in territory stability that suggest these patterns vary among species (Morton et al. 2000, Fedy and Stutchbury 2004, Gill and Stutchbury 2006, Stouffer 2007). For example, Buff-breasted Wrens (*Cantorchilus leucotis*) show high territory fidelity even in the presence of available territories, which appears to be dictated by territory and mate fidelity established once a pair breeds together (Gill and Stutchbury 2006). Conversely, White-bellied (*Myrmeciza longipes*) and Dusky (*Cercomacroides tyrannina*) antbirds frequently abandon territories, although White-bellied Antbirds more often maintain territories located in densely populated areas, suggesting territory stability may vary with territory quality (Morton et al. 2000, Fedy and Stutchbury 2004). In other species, territory stability is thought to be socially regulated or tied to competition for resources (Greenberg and Gradwohl 1986, Levin 1996a, Morton et al. 2000, Gorrell et al. 2005). However, territory density is low in other tropical resident species, which raises questions about what drives territoriality in a wide range of tropical

species (Stouffer 2007, Losada-Prado et al. 2014, Mathias and Duca 2016).

In Troupials, pair bonds and territories were stable even though the landscape was not saturated (Fig. 1). This may be counter to expectations: if space is available, high rates of territory movement or switching may be expected (Gill and Stutchbury 2006). Territory stability in the face of territory availability has been attributed to variation in territory quality or low instances of floaters (Morton et al. 2000, Fedy and Stutchbury 2004). We observed large numbers of floater individuals at our study site, however, including both males and females (although male floaters were more common; Odom, pers. obs.). We also observed higher territory density in the northern half of our study site, which corresponded to high densities of cacti, tamarind, and mesquite trees (preferred foraging habitat for Troupials at our study site; KJO, pers. observ.). Therefore, food availability may be a leading factor impacting territory value and occupancy in Troupials, although territory familiarity could also be important for retainment (Gill and Stutchbury 2006). Species-specific studies quantifying the extent of year-round territoriality and territory function are an important part of tropical bird biology and especially relevant for evaluating selection pressures on elaborate traits, like coloration, complex songs, and duets (Macedo et al. 2008, Tobias et al. 2011).

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